

Enchisthenes hartii.

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Enchisthenes Andersen, 1906

Enchisthenes Andersen, 1906:419. Type species *Artibeus hartii* Thomas, 1892, by original designation.

CONTEXT AND CONTENT. Order Chiroptera, Suborder Microchiroptera, Family Phyllostomidae, Subfamily Phyllostominae, Tribe Stenodermatini (Baker et al., 1989). This is a monotypic genus.

Enchisthenes hartii (Thomas, 1892)

Hart's Little Fruit Bat

Artibeus hartii Thomas, 1892:409. Type locality "Botanic Gardens, Trinidad" (restricted to Botanic Gardens, Port-of-Spain, Trinidad by Thomas—1893).

Enchisthenes hartii: Andersen, 1906:419. Generic description and name combination; type species *Artibeus hartii* Thomas, 1892, by monotypy.

Dermanura hartii: Owen, 1987:47. Name combination.

CONTEXT AND CONTENT. Context as for the genus. No subspecies are recognized (Arroyo-Cabral and Owen, 1996).

DIAGNOSIS. Allied to *Artibeus* but crown of inner upper incisors simple (not bifid); M3 in row, situated directly behind M2, and as broad as the posterior margin of M2; m3 comparatively large, about $\frac{1}{4}$ size of m2; well developed M3/m3 affects the form of the surrounding bone (Miller, 1907); metacone and metaconule of M2 set apart as distinct lobes by a deep fissure (Marques, 1993); tragus with a pointed projection on the inner margin, about 1 mm below the tip (Andersen, 1908).

GENERAL CHARACTERS. Skull short and broad (Fig. 1); profile from front of sagittal crest to nasals concave; palate short and anterior margin of mesopterygoid fossa V-shaped; cutting edges of upper median incisors simple, obtusely pointed in the center, without any indication of a notch; outer upper incisors narrower and shorter, cutting edge simple; lingual cusp of P4 absent or poorly developed; condylar process prominent, projecting conspicuously from ramus (Goodwin, 1940; Marques, 1993).

Upper parts dark brown, almost blackish on head and shoulders; underparts paler than back, darkest anteriorly (Hall, 1981). Face and head to back of ears almost black, marked by two narrow "buffy brown" stripes about 12 mm long that extend posteriorly from nose-leaf to crown just beyond margin of pinnae (Sanborn, 1933; Fig. 2). Distal edges of pinnae are lighter.

Upper side of proximal two-thirds of forearm, the entire interfemoral, and upper side of tibia and foot densely haired; a tuft of very short hairs on the metacarpal of the pollex (Andersen, 1908). Nose-leaf relatively short and broad, the width at base being almost equal to $\frac{1}{6}$ its length from nostrils to tip (Andersen, 1908), length:width index about 1.00 (1.00–1.10; Marques, 1993). Medial edges of both lips have cone-shaped papillae, with the lower lip including well-defined warts (Albuja, 1982). Plagiopatagium attached at ankle (Marques, 1993). Interfemoral membrane extremely short, about 3–4 mm along its mid-line. The wing-index does not differ from that of *Artibeus*; the second phalanx of the third digit is relatively short, less than 1.5 times the length of the first phalanx (Andersen, 1908).

Means of measurements (in mm), followed by ranges in parentheses, for 13 specimens (unless otherwise noted) from Costa Rica are as follows: length of forearm, 40.1 (37.0–42.6; n = 19); greatest length of skull, 20.8 (20.2–21.9); condyllobasal length, 18.8 (18.0–19.8; n = 12); zygomatic breadth, 12.4 (11.7–12.9); mastoidal breadth, 10.7 (9.9–11.3); breadth of braincase, 9.6 (9.3–10.0); width of postorbital constriction, 6.0 (5.6–6.7); breadth



FIG. 1. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of *Enchisthenes hartii* from Trinidad, St. George Co.; Maracas Valley (male, Texas Tech University 5243). Greatest length of skull (including incisors) is 20.5 mm; greatest length of mandible (including incisors) is 12.8 mm.



FIG. 2. *Enchisthenes hartii* from Tingo Marfa, Huanuco, Perú. Photograph provided by R. J. Baker.

across M2-M2, 8.5 (8.1-8.8); length of maxillary toothrow, 6.9 (6.7-7.2); length of mandibular toothrow, 7.2 (7.0-7.5—Gardner et al., 1970). Averages for external measurements for 39 males and 36 females, respectively, from northern South America, are: total length, 60.3, 61.0; length of hind foot, 12.1, 12.0; length of ear, 15.9, 15.8; length of forearm, 39.2, 39.2; mass, 17.4, 17.3 g (Eisenberg, 1989).

Little difference was found between specimens from Trinidad and northeastern Mexico, and no geographic variation was obvious (Baker and López, 1968). There is no detectable sexual dimorphism in this species (Eisenberg, 1989; Swanepoel and Genoways, 1979). No geographic pattern was found in cranial variation in a study of most specimens available from North American museums by Arroyo-Cabral and Owen (1996), nor did they detect sexual dimorphism in size within any of their population samples.

DISTRIBUTION. *Enchisthenes hartii* is an unusually widespread species (Fig. 3), occurring from north-central Mexico southward through Central and South America to Bolivia east of the Andes and to Ecuador west of the Andes (Hall, 1981; Handley, 1987; Koopman, 1982). There is an extrazonal record from Arizona, but this specimen may have been unintentionally imported (Irwin and Baker, 1967). *E. hartii* is considered uncommon to rare throughout most of its range, although it is apparently abundant at some localities in South America (Arroyo-Cabral and Owen, 1996). It is unclear whether the distribution is continuous throughout its range, or whether the reported populations are in fact disjunct, as could be indicated by the absence of specimens from Nicaragua (Jones and Owen, 1986), northern Colombia, and north-central Peru. A list of localities was provided by Arroyo-Cabral and Owen (1996) for most specimens housed in North American mammal collections and for some deposited in South American museums.

Enchisthenes hartii occurs from near sea level to more than 3,500 m in elevation. Collecting records indicate a greater abundance at moderate to higher elevations in Mexico, Costa Rica (1,900 to 2,600 m—Gardner et al., 1970), Venezuela (1,000 to 2,250 m—Handley, 1976), and Peru (850 to 3,540 m—Anderson et al., 1982; 400 to 1,700 m—Pacheco et al., 1993). In Central America, McCarthy et al. (1993) noted that this species is montane, restricted to the uplifted regions of Chiapas-Guatemala, El Salvador, Honduras, and Costa Rica-Panama, where the majority of specimens were obtained from localities above 1,500 m (74.4%—McCarthy and Bitar, 1983). In Chiapas, Mexico, *E. hartii* inhabits lowlands (<1,000 m—Alvarez-Castañeda, 1993). However, several specimens have been collected at localities up to 1,740 m in Chiapas (Arroyo-Cabral and Owen, 1996).

FORM. Based on wing-derived variables, *E. hartii* is similar to *Sturnira ludovici*, *Platyrrhinus brachycephalus*, *Ardops nichollsi*, and a then-undescribed species of *Artibeus* (Smith and Starrett, 1979). The only reported dental abnormalities are missing lower incisors and bifid first upper incisors (Farney, 1976).

REPRODUCTION. *Enchisthenes hartii* appears to be reproductively active throughout the year, but it may undergo a period

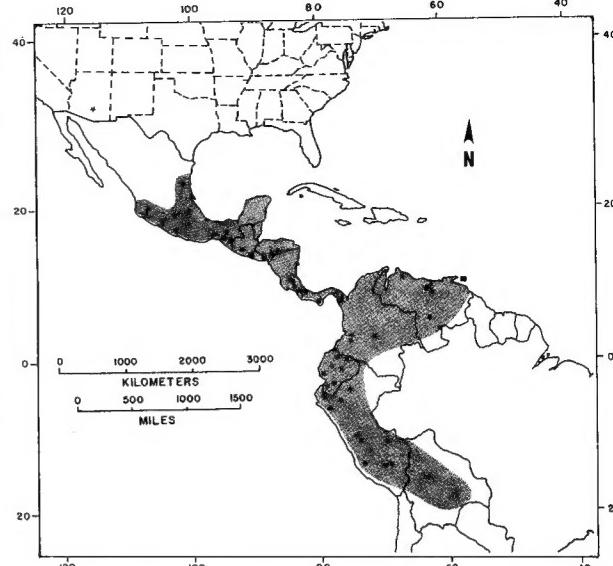


FIG. 3. Distribution of *Enchisthenes hartii*, modified from Hall (1981) and Koopman (1982). Stars indicate known collecting localities as listed in Arroyo-Cabral and Owen (1996).

of reproductive inactivity that is not apparent because data are not available from all months of the year at each locality (Wilson, 1979). Reproductive quiescence was corroborated by Thomas (1972) for populations from southwestern Colombia, where he collected pregnant individuals during May over several years but found no pregnant females in December. Pregnant females have been collected in January, May, and June in Costa Rica (Gardner et al., 1970), and in February in El Salvador (Hellebuyck et al., 1985). Lactating females are known from May, June, July, and August in southern Mexico and Costa Rica (Armstrong, 1969; Baker et al., 1971; Gardner et al., 1970).

ECOLOGY. Individuals of *E. hartii* have been collected mostly in open spaces, either in flyways or over water (Handley, 1976; Jones, 1964; McCarthy and Bitar, 1983; Ramírez-Pulido and López-Forment, 1979), or close to tree crops (de la Torre, 1955; LaVal, 1969), and sometimes under inclement conditions such as rain (Baker et al., 1971) or wind (Baker and López, 1968). Collecting sites were in hardwood forests with dense understory (Baker and López, 1968; McCarthy and Bitar, 1983), cloud forest (Baker et al., 1971; Handley, 1976; Hellebuyck et al., 1985), evergreen forest (Handley, 1976; Webster and Jones, 1980), tropical deciduous forest (LaVal, 1969), pine-oak forest (Jones, 1964), and caletal (Armstrong, 1969). In northern South America, this species is strongly associated with moist habitats and stratified tropical evergreen forest, but it does occur in cloud forest, and some specimens were taken in dry deciduous forest (Eisenberg, 1989). One specimen (from Arizona) was found under the eaves on the west side of a house at an elevation of 730 m (Irwin and Baker, 1967).

Other bats netted with *E. hartii* include (Emballonuridae) *Rhynchonycteris naso*; (Mormoopidae) *Pteronotus davyi*, *P. gymnonotus*, *P. parnelli*; (Phyllostomidae—Desmodontinae) *Desmodus rotundus*; (Phyllostomidae—Micronycterinae) *Micronycteris megalotis*; (Phyllostomidae—Phyllostominae) *Anoura cultrata*, *A. geoffroyi*, *Artibeus jamaicensis*, *A. lituratus*, *A. obscurus*, *A. planirostris*, *Carollia castanea*, *C. perspicillata*, *Centurio senex*, *Chiroderma salvini*, *C. trinitatum*, *Choeroniscus minor*, *Dermanura anderseni*, *D. azteca*, *D. glauca*, *D. tolteca*, *Glossophaga commissaris*, *G. soricina*, *Hylonycteris underwoodi*, *Lonchophylla robusta*, *Platyrhinus helleri*, *Rhinophylla pumilio*, *Sturnira erythromos*, *S. lilium*, *S. ludovici*, *S. magna*, *S. mordax*, *Tonatia minuta*, *Uroderma bilobatum*, *Vampyressa macconnelli*; (Vesperilionidae) *Eptesicus furinalis*, *E. fuscus*, *Lasiurus borealis*, *L. intermedius*, *Myotis chiloensis*, *M. keaysii*, *M. nigricans*; and (Molossidae) *Molossus molossus* (Anderson et al., 1982; Baker and López, 1968; Gardner, 1976; Gardner et al., 1970; Hellebuyck et al., 1985; Jones, 1964; LaVal, 1969; McCarthy and Bitar, 1983;

Ramírez-Pulido and López-Forment, 1979; Webster and Jones, 1980).

Specimens of *E. hartii* from southwestern Colombia taken from April to August were feeding almost exclusively on small figs (*Ficus*), indicating that the fruiting of such trees may cause the species to concentrate periodically in certain areas (Thomas, 1972). *E. hartii* was observed to be common in *Ficus* groves, potentially making it easy prey for owls (de la Torre, 1955). Fruits eaten were small, about a centimeter in diameter. The only reported predators of this bat were unidentified owls, since remains were found in owl pellets in Tamaulipas and Ecuador (Goodwin, 1940, 1954).

Ectoparasitic mites occurring on *E. hartii* include *Periglischrus iheringi* (Mesostigmata, Spinturnicidae) from Panama (Furman, 1966) and Venezuela (Machado-Allison, 1965), and *Macrolyssoides* sp. (Mesostigmata, Macronyssidae) from Panama (Radovsky, 1967). Specimens from southwestern Colombia were negative when tested for *Salmonella* and *Shigella* infections and histoplasmosis (Arata et al., 1968; Tesh et al., 1968).

GENETICS. Chromosomal and fundamental numbers are 30–31 and 56, respectively. All chromosomes are biaxed, with eight pairs (large to small) either metacentric or submetacentric, and six subtelocentric pairs, ranging in size from large to medium; the X chromosome is subtelocentric and the Y is submetacentric-acrocentric (Baker, 1967; Baker and Hsu, 1970). The karyotype of *E. hartii* can be derived from that of *Artibeus* (*sensu lato*) by a reciprocal translocation involving pairs 13 and 14 (or perhaps 8 instead of 14), changing a medium (pair 13) and a small-sized metacentric (pair 14) to two medium-sized subtelocentrics (Baker et al., 1979).

Enchisthenes hartii shares neither a 900-bp nuclear satellite DNA with *Artibeus*, *Koopmania*, and *Dermanura*, nor a nuclear satellite DNA of 400–500 bp with *Dermanura*. Nor does the level of sequence divergence of the mitochondrial cytochrome *b* in *E. hartii* affiliate it with these taxa (Van Den Bussche et al., 1993).

REMARKS. The taxonomic position of this species has an unsettled history. *Enchisthenes hartii* was described by Thomas (1892) as a species of *Artibeus*. Subsequently, the species was removed from *Artibeus* and placed in a new monotypic genus *Enchisthenes*, based on several characters that Andersen (1906) considered to be distinctively diagnostic. For more than 60 years, Andersen's taxonomy was followed by most authors, until Goodwin (1969) noted that the diagnostic characters of the genus (cutting edge of the inner lower incisors and presence of upper and lower m3) were not unlike those of some members of the genus *Artibeus*. *Enchisthenes* and *Artibeus* were therefore regarded by him as congeneric. This taxonomic arrangement previously had been proposed, without comment, by Simpson (1945), and it was followed by Koopman (1978) and others (see Arroyo-Cabral and Owen, 1996). Subsequently, in a revision of the bats of the tribe Stenodermatini, *A. hartii* was tentatively allocated, along with several other species formerly classified as *Artibeus*, to the resurrected genus *Dermanura* (Owen, 1987).

Recently, based on nuclear satellite DNA and sequence data for mitochondrial cytochrome *b*, *D. hartii* was characterized as genetically distinct from *Artibeus*, *Dermanura*, and *Koopmania* (Van Den Bussche, 1993), but these authors did not offer a formal taxonomic proposal to assign the species to any generic name. At the same time, based on morphological data supplemented with karyotypic results, another taxonomic analysis of the genera of the tribe Stenodermatini resulted in no support for recognition of *Enchisthenes* as a genus distinct from *Artibeus* (Lim, 1993). Finally, based on cluster and ordination analyses of morphometric characters of *Dermanura* species and *Koopmania concolor*, *D. hartii* was found to be the most phenetically distinct species within that assemblage (Arroyo-Cabral and Owen, 1996). Based primarily on the results of Van Den Bussche et al. (1993), reapplication of the specific name *Enchisthenes hartii* was proposed, and the synonymy was provided (Arroyo-Cabral and Owen, 1996).

The holotype is housed at the British Museum of Natural History and cataloged as BMNH 92.9.7.8, juvenile male, in alcohol, skull removed, date of collection not specified on label. The skin is in poor condition and the skull is damaged (Carter and Dolan, 1978).

The generic epithet *Enchisthenes* means "armed with a spear," in allusion to the form of the erect portion of the nose-leaf

(Andersen, 1906). The specific name honors Mr. J. H. Hart, Superintendent of the Botanic Gardens, Trinidad, the person who presented a collection of bats to the British Museum, including that referred as the holotype of *Enchisthenes hartii* (Thomas, 1892).

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